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Seagrass blue carbon dynamics in the Gulf of Mexico: Stocks, losses from anthropogenic disturbance, and gains through seagrass restoration

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ABSTRACT

Seagrasses comprise a substantive North American and Caribbean Sea blue carbon sink. Yet fine-scale estimates of seagrass carbon stocks, fluxes from anthropogenic disturbances, and potential gains in sedimentary carbon from seagrass restoration are lacking for most of the Western Hemisphere. To begin to fill this knowledge gap in the subtropics and tropics, we quantified organic carbon (C_{org}) stocks, losses, and gains from restorations at 8 previously-disturbed seagrass sites around the Gulf of Mexico (GoM) (n = 128 cores). Mean natural seagrass C_{org} stocks were 25.7 ± 6.7 Mg C_{org} ha^{-1} around the GoM, while mean C_{org} stocks at adjacent barren sites that had previously hosted seagrass were 17.8 Mg C_{org} ha^{-1}. Restored seagrass beds contained a mean of 38.7 ± 13.1 Mg C_{org} ha^{-1}. Mean C_{org} losses differed by anthropogenic impact type, but averaged 20.98 ± 7.14 Mg C_{org} ha^{-1}. C_{org} gains from seagrass restoration averaged 20.96 ± 8.59 Mg ha^{-1}. These results, when combined with the similarity between natural and restored C_{org} content, highlight the potential of seagrass restoration for mitigating seagrass C_{org} losses from prior impact events. Our GoM basin-wide estimates of natural C_{org} totaled ~ 36.4 Tg for the 947,327 ha for the USA-GoM. Including Mexico, the total basin contained an estimated 37.2–37.5 Tg C_{org}. Regional US-GoM losses totaled 21.69 Tg C_{org}. C_{org} losses differed significantly among anthropogenic impacts. Yet, seagrass restoration appears to be an important climate change mitigation strategy that could be implemented elsewhere throughout the tropics and subtropics.

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1. Introduction

Seagrasses are a critical, but continually-diminishing blue carbon foundation habitat. The IPCC (Intergovernmental Panel on Climate Change) Wetlands Committee only recently recognized that wetlands and submerged aquatic vegetation including marshes, mangroves, and seagrasses contribute significantly to the global stored carbon sink, and Hiraishi et al. (2014) called upon governments to implement more sophisticated inventories of wetlands carbon emission factors to move beyond the use of basic default values for tidal wetlands (140 g^{-2} y^{-1}) and basic equations (i.e., Tier I standards). Current baseline estimates indicate that global seagrass carbon pool lies between 4.2 and 8.4 Pg of organic carbon (C_{org}) (Fourqurean et al., 2012a). Yet, these important seagrass blue carbon sinks continue to be lost at an alarming rate (Waycott et al., 2009). Given that blue carbon sequestration rates can be orders of magnitude higher than terrestrial carbon pools (Fourqurean et al., 2012a), information about seagrass blue carbon cycling is an important factor in IPCC decision-making and carbon accounting. Presently, regional subtropical and tropical seagrass blue carbon stock data remain sparse for seagrass and we lack a coherent fingerprint of the spatial variation in C_{org} stocks in relation to local environmental influences. Nor do we understand the potential of seagrass restoration for bolstering blue carbon stocks in these regions. Such information is critical for achieving long-term Tier II (regional/country-specific emission factor values) and Tier III (more complex, site-specific emission factor values) blue carbon accounting goals and REDD + (reducing emissions from deforestation and forest degradation) carbon offset eligibility.

1.1. Seagrass blue carbon losses from anthropogenic disturbances

C_{org} fluxes from seagrass die-off after anthropogenic disturbance events can vary considerably depending on local environmental conditions, C_{org} inputs to the estuary, and the type and magnitude of the disturbance (Macreadie et al., 2013). Pendleton et al. (2012) generated a rough global estimate of blue carbon emissions from conversion and degradation of coastal marine vegetation. However, their estimates utilized default mean C_{org} stock values of 140 Mg ha^{-1} from Fourqurean et al. (2012a), and they did not incorporate spatial variation in sedimentary carbon stocks or the effects of different types of impacts on seagrass C_{org}-cycling. Several researchers have presented site-specific data on seagrass carbon flux from human impacts including Marbà et al. (2015) in Western Australia on the Indian Ocean

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at a location where the seagrass ecosystem sediment collapsed resulting in the disappearance of the seagrass carbon and its associated sediments in response to disturbance. Likewise, Macreadie et al. (2014) experimentally disturbed the sediment in small plots, and measured sediment carbon content over 24 months in central eastern Australia, but found no significant C_{org} loss. Such results highlight the need for more studies that address the mechanisms of seagrass carbon cycling following anthropogenic disturbances. The few existing empirical studies on seagrass blue carbon losses suggest that making common assumptions about coastal marine carbon cycling can be misleading (Macreadie et al., 2014).

1.2. Seagrass restoration as a climate change mitigation strategy

van Katwijk et al. (2016) demonstrated the importance of seagrass restoration on a global-scale for restoring coastal marine ecosystem services, yet the effects of restoration activities on blue carbon cycling have yet to be examined fully. Seagrass restoration theoretically provides one potential solution for mitigating the losses of blue carbon stocks from anthropogenic disturbances. Yet, few prior studies have examined the potential of seagrass restoration for bolstering blue carbon stocks. To date, data exist from only two sites (Chesapeake Bay, USA (Greiner et al., 2013) and Perth, Western Australia (Marbà et al., 2015)) that quantify the effects of seagrass restoration on seagrass sedimentary carbon stocks. The results of both studies indicate that C_{org} stocks in restored areas following seagrass die off from anthropogenic impacts can vary considerably. These studies represent two disparate data points from one temperate high energy site on Western Australia's Indian Ocean and one temperate Atlantic estuarine site in Chesapeake Bay, USA. Regional-scale studies of the effects of multiple seagrass restorations on blue carbon stocks under a variety of environmental and anthropogenic stressors are clearly needed for achieving detailed and regional-scale Tier II and III IPCC carbon accounting goals.

This study builds upon the limited body of literature on seagrass sedimentary carbon accounting via a regional-scale analysis of seagrass C_{org} stocks, losses from an array of anthropogenic disturbances, and C_{org} gains through multiple seagrass restorations across the USA GoM. Our overarching goal was to examine the dynamics of seagrass sedimentary carbon flux from disturbance and to evaluate the potential of subtropical/tropical seagrass restoration as a climate change mitigation strategy. We hypothesized that the effects of different types of seagrass disturbances on C_{org} losses would vary in accord with the disturbance type, and that different types of disturbances would also influence the subsequent carbon sequestration potential of seagrass beds that were then restored after such impacts. We also hypothesized that seagrass restoration would bolster blue carbon stocks in barren areas where seagrass die-off had previously occurred. We tested these hypotheses by systematically collecting C_{org} data from across 8 subtropical/tropical seagrass sites that had all been restored using a consistent restoration methodology across the USA GoM, which is considered a of North American carbon hotspot (Hofmann et al., 2008; Herrmann et al., 2015). Each sample site had experienced major seagrass die-off from an anthropogenic disturbance, and then Thorhaug subsequently restored portions of each site using standardized restoration methods over the last 4 decades in a series of restorations (see Table 1 for descriptions of individual restoration projects). The present study uses known seagrass kill dates (i.e. the dates of closing of thermal and sewage effluents, vessel groundings, and artificial-fill dates of US Army Corps of Engineers) and the exact restoration dates to estimate C_{org} losses and gains at 8 sites across the USA GoM (Table 1 contains descriptions of each study site and its anthropogenic impact). The dates of both the impact event and the restoration date, provided a fine-scale clock for quantifying both C_{org} losses since disturbance and gains since restoration.

Table 1
Site information for eight Gulf of Mexico seagrass sample sites. All sites contained the four treatment blocks including natural seagrass, restored seagrass, impacted barren areas that were never restored, and always barren sites. The age (y) of each restoration, species composition, spatial location, sediment type, and impact type are listed for each location.

Restoration age & species	Sites & location	Sediment type, GIS	Impact type with age; restoration age & citations
42 y *Thalassia testudinum*, *Halodule wrightii*	Turkey Point, S. Biscayne Bay, FL. Abundant Mangroves 252,510.88 N 801,934.09 W	Medium quartz sand	Heated effluent (1969–71) Bader et al. (1970). Planting 1973 by Thorhaug (1974).
32 y *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*	24–27th Street NE N. Biscayne Bay, FL 254,352.35 N 801,233.19 W	Course quartz sand	Sewage (ended 1958) McNulty (1970) Planting 1983, Thorhaug (1985)
37 y *Thalassia testudinum, Halodule wrightii*, *Syringodium filiforme*	*N. Julia* Tuttle (36th St) Causeway, N. Biscayne Bay, FL Mangroves present 254,840.54 N 801,003.66 W	Rock and rubble overlain with quartz sand. Constructed causeway.	Dredge & filled construction (1959) Chardon (1976). Planting 1978 by Thorhaug (1980a)
29 y *Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*	Grove Isle, Central Biscayne Bay, FL, Sparse mangroves present 254,342.11 N 801,302.72 W	Quartz sand	Dredge and fill (early 1961), Harlem (1979), Planting 1985 by Thorhaug (1987)
15 y *Halodule wrightii*, *Halophila decipiens*	Predator Island, E. Northern Laguna Madre, TX Adjacent marshes. 273,220.22 N 971,113.41 W	Quartz Sand. Scrape down of former dredge island.	Fill for Channelization, (1947) artificial island scrape-down (1998). Planting 1999, Thorhaug (2001)
1 y *Halodule wrightii*	Shamrock Shoreline, East Corpus Christi Bay, TX. Adjacent marshes. 274,516.74 N 970,927.16 W	Sand, quartz, oyster shell plus clay.	Filled causeway & shoreline & oil spill 1942's. Planting 2013 by Thorhaug (2014)
2 y *Halodule wrightii*	San Luis Pass, Galveston Bay, TX. Adjacent marshes. 290,551.61 N 950,638.06 W	Sand. Quartz.	Fill 1969 (TX Handbook) Planting, 2013 Thorhaug (2014)
1 y *Halodule wrightii*	Aransas/St Charles Bay, TX. 280,851.94 N 965,819.81 W	Sand quartz, with marsh Peat underlying	Lg. Salinity (2011–3), bridge construction (2011–13), Shoreline fill (2005–2013). Aluminum railings. Planting 2013 by Thorhaug (2014)

2. Study region

2.1. Gulf of Mexico seagrasses

The GoM is an internal North American basin, that is dominated by sedimentary estuaries that contain seagrasses as a foundation habitat throughout the basin. Soft sandy and muddy bottoms are characteristic of estuaries across the region, and these wetlands support large expanses of seagrasses, marshes, and mangroves. Two benthic western Florida shelves also support seagrass. Seagrasses extents in the USA GoM have been estimated at near 1 million ha (chiefly found in Florida and in Texas's Laguna Madre (Appendix A) (Duke and Kruczynski, 1992; Pulich and Hardegree, 2006; Handley et al., 2007; Yarbro and Carlson, 2011) with rough estimates of 25,000 ha in the Mexican portion (Green and Short, 2003). Seagrass productivity is high in the GoM due to its year-long growing season and clear waters (Thorhaug et al., 1978; Dunton, 1994; Livingston et al., 1998). Extensive anthropogenic development has occurred chiefly during the last century, which has decimated intertidal wetlands and seagrasses throughout the region. Duke and Kruczynski (1992) estimated that 54% (19,250 km^2) of all wetlands and seagrasses in the GoM were lost by 1992. To date, this seagrass loss was considered to chiefly affect fisheries and habitat extent. However, such losses likely also have effects on GoM seagrass carbon capture and storage.

3. Methods

3.1. Field methods

Field sampling took place at low tide during the summer and early fall of 2014 at all sites. At each sample site, quadruplicate 7-cm radius and 20-cm deep sediment cores were collected from the following treatments: (1) "always barren" (AB) over 50 y; (2) naturally-occurring seagrass (NS) for over at least 50 y; (3) "impacted barren" (IB) former seagrass meadows killed by the disturbance but receiving no restoration and is still barren of seagrass in 2014, and (4) restored seagrass (RS) (Table 1). The 16 cores at each sample site (4 per treatment) were taken at 7.5-m intervals along a transect that ran through the center of each treatment type and parallel to the current at ~ 0.75 to 1 m water depth (n = 128 cores). Transects were run through the center of each treatment to minimize edge effects from prior seagrass die-off. All four treatments (AB, NS, IB, and RS) were present in patches within each sample site, and the NS, IB, and AB patches at each site were all located within a 650-m radius from each restoration site. Temporal changes in seagrass cover were estimated prior to going in the field using historical aerial imagery (https://coast.noaa.gov/dataregistry/search/collection). Seagrass die-off, or loss, generally occurred simultaneously at each site at a known date in response to a known disturbance event. These seagrass die-off dates or "clocks" indicated the time of the vessel (2 sites), fill (3 sites), stoppage of effluents (2 sites), or salinity modification event (1 site) that impacted each seagrass meadow, after which natural sediment accumulation presumably resumed. A second "clock" was the known time of planting each site.

We chose a coring depth of 20 cm based on the rooting depths of *Thalassia testudinum* and *Halodule wrightii* and published accretion rates for Biscayne Bay, Corpus Christi, and Galveston Bay in nearby seagrass beds (Wingard et al., 2003; Yeager et al., 2006; Ravens et al., 2009), which suggested that a 20 cm deep core would capture the carbon lost from a 60-year-old impact event and the carbon gained from a 40-year-old restoration (the oldest restoration). Our field observations further justified this sediment core depth because the anthropogenic impact and subsequent sediment restoration layers were visible in our restored seagrass sediment cores as large changes in sediment texture, composition, and color at various sample depths at sites within the 20 cm IB and RS cores.

Samples were immediately extruded after coring, put on ice in the field, and then immediately refrigerated at -4 °C upon return from the field until processing immediately after collection to prevent microbial processes from metabolizing the carbon. Sediments in most cores were aluminosilicate sand and they experienced little compaction from coring. However, some cores did show evidence of sediment compaction (11% of all cores taken), and for those cores, we applied compaction correction factors prior to sectioning cores for further sediment analysis following Howard et al. (2014). Cores were sectioned and homogenized immediately upon return from the field at three sampling intervals per core including 0–5 cm, 10–15 cm, and 10–20 cm depths (n = 384). Shells, rocks, and large rhizomes were removed prior to subsequent C analyses.

3.2. Lab methods

In the lab, samples were transferred into pre-weighed 15 mL centrifuge tubes, and wet sediment volumes were recorded after centrifugation at 3000 rpm for 8 min. Samples were then dried at 70 °C to a constant mass and the dry bulk density (BD) was estimated by dividing the dry mass of each sediment section by the wet volume. Dried 0–5 cm, 5–10 cm, and 10–20 cm samples were homogenized using a mortar and pestle and transferred to 20 mL glass scintillation vials (n = 384). Carbon analyses followed procedures outlined by Howard et al. (2014). Loss on ignition (% OM), and total and inorganic carbon (% C_{tot}, % C_i) were measured on a CE Elantech Flash 1112 Elemental Analyzer (n = 768). Inorganic carbon measurements were completed after a loss on ignition (LOI) measurement where ~ 500 mg subsample was ashed in a muffle furnace at 500 °C for 5 h. Inorganic carbon results were then scaled to the original dry sediment masses by using ash to sediment weight ratios. The percentage of organic carbon (C_{org}) was calculated as the difference between Ci and C_{tot}. Total C_{org} density (Mg C_{org} ha^{-1}) and total organic carbon standing stock were estimated using the methods described in Howard et al. (2014).

3.3. Statistical analysis

Data were examined for normality and transformed as necessary prior to analysis. We used mixed models and the nlme package of R for analyzing differences in % C and C_{org} content among treatments, disturbance types, sample site regions, and restored seagrass bed ages. Differences in % C_{org} were also evaluated over the depth profiles of each treatment via mixed models. In all analyses, cores were nested within each site-treatment combination to account for the covariance structure in the nested sampling design. Significant differences were assessed among the following site and treatment combinations:

- Treatment-level differences in C_{org} (NS, RS, IB, vs. AB).
- C_{org} depth by treatment differences in carbon content.
- Species-level differences in sedimentary C_{org}, with core nested within treatment.
- Differences among sample sites in natural vs. restored C_{org} by region and restoration age: young (≤ 3 years), intermediate (≥ 4–15 years), and old (> 15) since restoration.
- Differences in restoration response by impact or disturbance type (dredge and fill, effluent, turbidity, thermal pollution, or salinity).

Sample sites and treatments were included as fixed effects. Random effects included the intercept, treatment-site relationships, and the core nested within sample site. The residuals of each model were inspected for deviations from homoscedasticity, and only models containing residuals without obvious deviations from normality were kept. We used linear regression to estimate the relationship between % OM and % C_{org} to assess the effectiveness of the LOI technique. Differences in C_{org} stocks between seagrass species (*T. testudinum* and *H. wrightii*) were tested via a Student's *t*-test.

Losses in C_{org} from anthropogenic impact and gains from restoration were calculated on a site-by-site basis using mean C_{org} stock values for the four cores in each treatment at each sample site for the entire 0–20 cm core. We followed methods employed by Macreadie et al. (2013) to assess variation in sediment bulk density across the depth profiles of the cores in each treatment, which indicated no significant differences among sample depths or treatments (Appendix A), and supported the assumption that the carbon stocks to this depth were comparable among sites. Thus, we estimated the loss in C_{org} from prior impact events that resulted in seagrass die-off by comparing the four different treatments (AB, IB, NS, and RS) at each sample site. Loss in C_{org} stock in the top 20 cm of the sediment due to seagrass die-off at each site was estimated as:

$$\begin{aligned}\text{Loss} = {} & \text{mean natural seagrass } C_{org} \\ & - \left(\text{mean impacted barren } C_{org} \right. \\ & \left. - \text{ mean always barren } C_{org}\right).\end{aligned}$$

This metric denotes the amount of carbon which has been lost via leakage or perturbation of sediment over the period between the impact when the seagrass bed was killed or removed by impact and our field sampling. The original natural seagrass bed at each site prior to the disturbance was the control for original bed and the spatial proximity of all four treatments within 650 m among each other makes this comparison possible. Our assumption here was that the impacted barren sediments did not biologically-actively continue to sequester C after seagrass was killed.

We estimated the C_{org} gained through restoration as the mean C_{org} among cores at each site in restored beds minus mean C_{org} in for the four impacted barren cores at each sample site. Values were reported as overall averages by treatment, impact type, and by restoration age (young - < 3 years old, intermediate - 4–15 years old, and old - > 15 years since restoration). Estimates were calculated using site-specific, fine-scale estimates of total gain and gain per year using total C_{org} stocks for each 20-cm core and by taking the difference in C_{org} in restored sites from C_{org} in natural seagrass sites at those same sites divided by the number of years since restoration.

4. Results

4.1. Seagrass organic carbon stocks among sites, restored vs. natural beds vs. barren

Organic carbon stocks (C_{org}) varied significantly among treatments and across the 8 USA GoM sites ($F = 3.84$, $P = 0.011$), and there was a highly significant relationship between LOI and % C_{org} (Figs. 1–3; Table 2). The mean C_{org} in the top 20-cm of the sediment for natural seagrass beds at the sample sites was 25.7 ± 6.7 Mg C_{org} ha^{-1}. Restored seagrass sites had higher mean C_{org} stocks (38.7 ± 13.1 Mg ha^{-1}) than natural beds, although differences were not significant. However, restored seagrass beds had significantly higher C_{org} than impacted-barren and always-barren areas ($P < 0.05$). The baseline (control) of each estuary carbon stock, the “always barren” samples, varied substantially among sites (from 4.11 to 35.61 Mg C_{org} ha^{-1}) and seagrass species (Fig. 2, Table 2), but the C_{org} stock sequestered in natural seagrasses was always above that barren estuarine baseline (AB) (Table 2).

4.2. Changes in C_{org} with sediment depth

The organic carbon density by depth results (Fig. 4) indicated that substantial carbon was no longer present for the 0–15 cm of upper sediment layer depths in impacted barren (IB) areas compared to their former carbon levels in the natural seagrass (NS) beds. In the upper 0–5 cm, IB C_{org} was not statistically different from AB. However, at 5–10 and 10–20 cm depths IB C_{org} was significantly higher than AB indicating that C_{org} was no longer present for the 0–15 cm of the upper sediment layer depths in impacted areas IB but that residual C_{org} was present in those cores at deeper sediment depths.

4.3. C_{org} gains from restoration and restoration age effects

Mean organic carbon gains through seagrass restoration were 20.96 ± 8.59 Mg C_{org} ha^{-1} across the sites for the top 20 cm of sediment. We note variable values by sample site location and by the age of the restored bed (Fig. 5, Table 2). C_{org} in restored sites differed significantly by restoration age (young - < 3 years old, intermediate - 4–15 years old, and old - > 15 years since restoration) ($F = 3.74$,

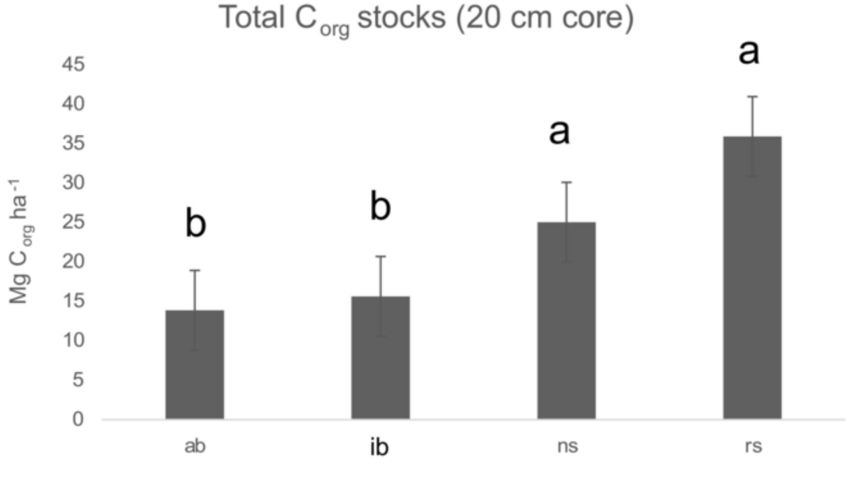


Fig. 1. GoM seagrass C_{org} content of natural seagrass (ns), restored seagrass (rs), always-barren (ab), and impacted-barren (ib) sediment. Values reported as means (± SE) across the 8 Gulf of Mexico estuarine sites. C_{org} differs significantly among treatments per a mixed model analysis ($P = 0.02$). Pairwise comparisons are shown with letters. Treatments not sharing letters significantly different $P < 0.05$-levels.

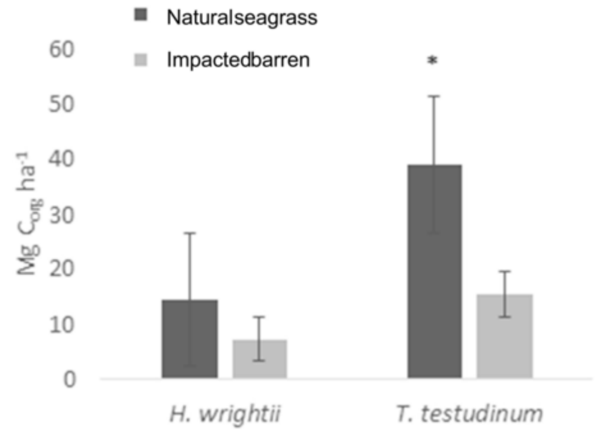


Fig. 2. Mean (± SE) organic carbon content of 20 cm cores from *H. wrightii* and *T. testudinum* natural seagrasses from 8 sampled Gulf of Mexico Sites vs. proximate previously-impacted seagrass meadow now barren. Significant differences ($P < 0.05$) among treatments and species are depicted with asterisks (*) according to a *t*-test.

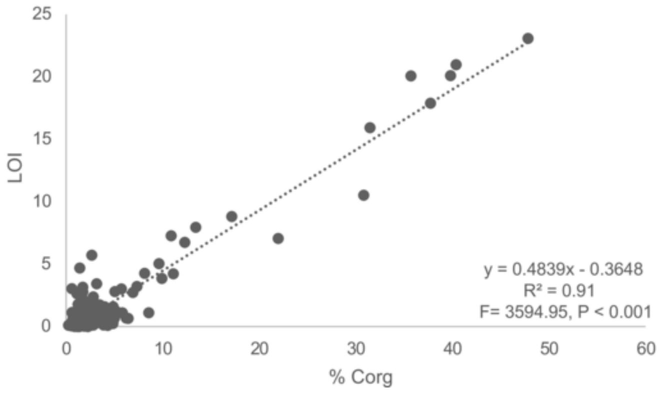


Fig. 3. Regression results between % C_{org} of the loss corrected percent weight of samples versus loss on ignition (LOI) from seagrass sediment samples from 8 sites in the Gulf of Mexico, including naturally occurring, restored seagrass, always barren and impacted barren sediment carbon values.

$P = 0.033$) and by location ($F = 6.34$, $P = 0.016$), but not by species (Figs. 2 and 5, Table 2). The intermediate age sites had the highest carbon accumulation rates per y (Fig. 5, Table 2).

4.4. C_{org} losses from impact and disturbance

Average organic carbon loss was 20.98 ± 7.14 Mg C_{org} ha^{-1} for the 8 sites across the USA Gulf of Mexico. Around the GoM basin, seagrass C_{org} loss varied significantly among impact types, species, and location (Table 2, Fig. 6, Appendixes B and C). The highest C_{org} losses (57.1 Mg C_{org} ha^{-1}) occurred at the Corpus Christi Oil & Gas site vessel grounding in Northern Laguna Madre, Texas. The lowest losses were at the San Luis Pass, Galveston Bay, Texas (2.91 Mg C_{org} ha^{-1}).

4.5. Pollutant-disturbance type effects

Seagrass organic carbon loss also differed among impact/disturbance types (Fig. 6). We also arranged differences among carbon into two groups: 1) where die-off from impact occurred once, but then seagrasses were conserved, and 2) sites that have continually experienced impact effects since initial seagrass die-off. The impact event type significantly influenced restored seagrass bed C_{org} stocks ($F = 21.2$, $P < 0.0001$). The site that experienced a sewage spill (36th St.) had the highest C_{org} gain following seagrass loss, whereas the high salinity site had lowest C_{org} stock following restoration (Aransas Bay). Seagrass meadows exposed to thermal pollution or vessel grounding, had intermediate C_{org} stocks that were similar among sites, although the vessel grounding occurred in south Texas (colonized by *H. wrightii*) and thermal pollution occurred in South Florida (colonized by *T. testudinum*). Both sites are now preserves, surrounded by natural shorelines and remain relatively undisturbed. The natural seagrass C_{org} at sites that were continually impacted even after the restorations had substantially lower C_{org} stocks (mean 11.7 Mg C_{org} ha^{-1}) than the once-impacted then-undisturbed sites (mean 42.5 Mg C_{org} ha^{-1}) both in Texas and Florida (Turkey Point, Predator, and Grove Isle). Natural seagrass C_{org} stocks were substantially lower than the C_{org} stock of barren sediment at the only once-impacted sites (Table 2).

4.6. Regional total C_{org} sequestration

The mean natural seagrass C_{org} sequestration was 39.2 ± 2.2 Mg C_{org} ha^{-1} for Florida (total $C_{org} = 34.7$ Tg) and 13.9 ± 8.3 Mg C_{org} ha^{-1} in Texas (total C_{org} 1.5 Tg). The average Texas C_{org} stock across sites that were restored 2 to 15 y ago was lower than older South Florida restored sites (35–42 y ago). Background C_{org} stocks in always barren sediments also differed significantly among disturbance-impact types and sites (Fig. 6, $P < 0.05$).

Florida had the highest regional C_{org} stock (21.6 Tg C_{org}) based on a seagrass extent of 850,874 ha (Appendix B), followed by Texas with 94,389 ha of seagrass (2.5 Tg C_{org}), and Alabama, Mississippi and Louisiana's combine extent of 1964 ha (0.049 Tg C_{org}). The seagrass C_{org} stock for the entire USA GoM was estimated by multiplying the mean C_{org} stock per ha by the federal/state government-measured spatial extents (see Table Appendix B for sources of spatial extent data) to obtain estimates of total regional C_{org} stock. When summed for the total stock across the USA GoM, we estimated a stock of 36.4 Tg C_{org} in seagrass sediments from the SE Florida tip to the Rio Grande US-Mexico border.

4.7. Regional GoM C_{org} losses

If the loss estimate is calculated as the "simple" product between mean spatial extent and mean global loss (i.e. Duarte, 2002; Fourqurean et al., 2012a), the estimated loss for the USA GoM would be 17.7 Tg C_{org}. The "simple" estimate differs by almost 20% from our "adapted" estimate of 21.69 Tg C_{org} found in the upper 20 cm of sediment across the USA GoM (Appendix C). We estimate that since WWII, using a series of governmental scientists' estimates of loss that the total spatial seagrass loss in the USA Gulf of Mexico is approximately 1,189,244 ha (see Appendix B for extents and references). We estimate a USA GoM-wide loss estimate of 21.69 Tg Corg during the past 50–75 y (Appendix C), although for Mexico's Yucatan Peninsula and northeastern GoM Mexican coast, there are no adequate seagrass spatial extent loss data.

5. Discussion

Our results demonstrate that sedimentary carbon stocks and fluxes vary in accord with the environmental setting of the estuary, species, impact type, and subsequent conservation status after restoration. Our study also highlights the importance of seagrass restoration as an important climate change mitigation strategy that has high potential for

Table 2
Study site sedimentary carbon characteristics for top 20 cm of sediment at the 8 GoM sample sites including organic carbon losses from impacts and gains from seagrass restoration measured in and adjacent to selected of the US GoM seagrass restoration sites of Thorhaug (1974, 1985, 2001, 2014) and Thorhaug et al. (1978). Seagrass bed health and protection status indicate whether the site has experienced continuous impact exposure over time or if it was subsequently put under conservation status. Impact event age indicates the number of years since the impacting event occurred that initially stimulated the seagrass die-off event.

Site	Seagrass health and protection status	State	Sedimentary C_{org} stock (Mg ha^{-1})				Impact event age (years)	Total C_{org} loss (Mg ha^{-1})	Restoration age (years)	C_{org} burial rate of restored beds (g m^{-2} y^{-1})	Total C_{org} gain (Mg ha^{-1})	C_{org} gain per year since restoration (Mg ha^{-1} y^{-1})
			Always barren	Impacted barren	Natural seagrass	Restored seagrass						
Turkey Point	Impacted then conserved	Florida	35.61	44.13	50.74	116.06	43	37.26	35	16.828	71.93	2.06
27th Street	Continually impacted	Florida	15.68	31.89	17.73	69.31	57	15.99	32	10.050	37.41	1.17
36th Street	Continually impacted	Florida	14.58	17.46	53.73	41.18	56	53.36	35	5.971	23.72	0.68
Grove Isle	Impacted then conserved	Florida	15.61	14.65	34.44	30.77	54	19.55	30	4.462	16.13	0.54
Predator	Impacted then conserved	Texas	6.70	5.77	17.87	13.69	90	17.68	16	2.054	7.92	0.50
San Luis Pass	Continually impacted	Texas	6.50	10.48	6.89	11.42	55	4.26	1	1.656	0.95	0.95
Shamrock	Continually impacted	Texas	10.94	13.28	19.54	22.87	65	11.82	2	3.431	9.60	4.80
Aransas Bay	Continually impacted	Texas	4.11	4.90	4.46	4.95	10	7.92	1	0.743	0.05	0.05

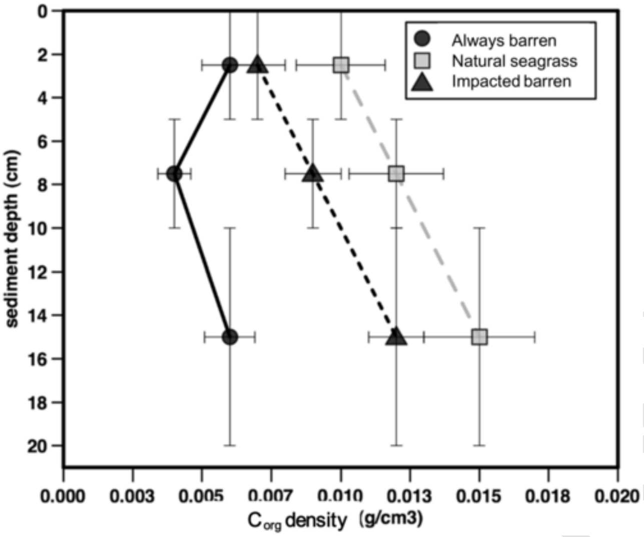


Fig. 4. Vertical depth core profiles of Gulf of Mexico seagrass of mean organic carbon (C_{org}) density (g/cm^3) comparing mean of treatments natural seagrass, always barren sites, and previously impacted but remaining barren sediment treatments at 8 USA GoM measured seagrass restoration sites. Horizontal bars represent standard errors for each depth interval. Vertical bars indicate the midpoint of the depth interval of each sample (i.e. 0–5 cm, 5–10 cm, or 10–20 cm). Abbreviations are: AB = always barren sites, IB = impacted barren-never-restored or revegetated sites; and NS = natural seagrass. AB C_{org} density differs significantly from NS and IB across all sediment depths, while IB Corg density is significantly lower than NS at only the shallower sediment depths according to mixed model analyses ($P < 0.05$).

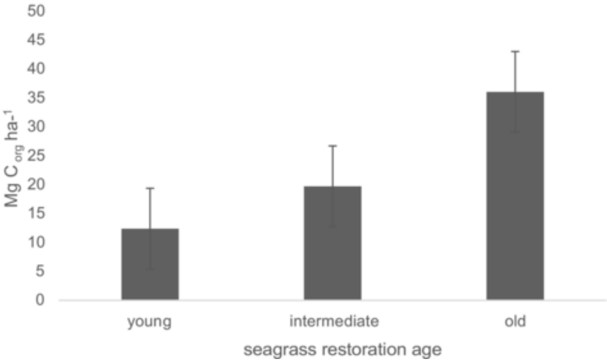


Fig. 5. Eight GoM seagrass restoration sites showing mean (± SE) organic C_{org} Mg ha^{-1} of young (< 2-year-old), intermediate (15–16-year-old), and older (38–43-year-old) restored seagrass sedimentary organic carbon. Older beds had significantly higher C_{org} stocks than young or intermediate restored sites, from the mixed model comparisons ($P = 0.0025$).

incorporation into carbon accounting schemes at the national- and regional-levels. Our regional-scale estimate of naturally-occurring seagrass sedimentary carbon stocks, loss from disturbance, and gains through restoration provide a first-time estimate of the C_{org}-cycling in seagrass across the GoM region. This regional-scale assessment relies on a systematic methodology of analysis, which uses a barren control to assess baseline C_{org} per at each estuary and consistently implemented restorations at each site. We added the natural barren background control as an important element for measuring the amount of loss of seagrass beds after impact, and for estimating the actual contribution of natural seagrass beds and seagrass restoration over background sedimentary carbon to the blue carbon budget.

While Lavery et al. (2013) and Duarte et al. (2013) have noted that seagrass blue carbon stocks and metabolism can display significant spatial heterogeneity, we demonstrated that both C_{org} losses and gains through restoration were similarly influenced by local environmental variation, by impact type, and by whether the site was subsequently preserved or continually disturbed after seagrass die-off. We showed that restored beds in areas that were initially lost from sewage effluents had significantly higher carbon stocks after restoration than seagrass areas that were lost and restored after dredge and/or fill impacts. We hypothesize this was probably a result of the high nitrogen and phosphate inputs associated with the sewage spills remaining in the sediment. Likewise, C_{org} stocks were lower in restored beds that were continuously disturbed or impacted following restoration than in beds that were impacted once and then conserved. Our ability to delineate this information hinged on our unique study design that included two seagrass treatments (natural and restored) and

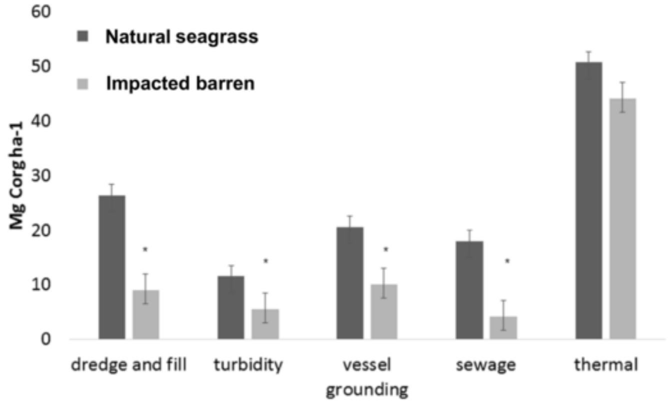


Fig. 6. Mean (± SE) sedimentary organic carbon stocks of natural vs. impacted barren (anthropogenically disturbed but never recolonized or restored) seagrass beds for different disturbance event types as treatments in 8 sampled sites the USA Gulf of Mexico. Treatments differed significantly ($P < 0.05$, depicted with asterisks) within each impact event type for dredge and fill, turbidity, vessel grounding, and sewage impact events according to the mixed effect model analyses.

two controls (historically-barren and presently-barren-previously-impacted) plus our intensive sampling regime at 8 sites around the USA GoM. These results also highlighted differences in background (barren) C_{org} stocks among estuaries, which suggests that natural baseline environmental carbon variation is an important factor in the C-sequestration potential of seagrass beds. For example, the Florida estuaries experience largely oceanic C inputs because of the lack of massive rivers that drain into those sites, while the Texas sites receive larger terrigenous riverine inputs from large watersheds. Likewise, the magnitude of the combined blue carbon sink differed among sites, with some estuaries having extensive adjacent marshes, some with mangroves and seagrass, and some with seagrass only, all of which differentially influence C_{org} stocks and cycling (Hemminga and Mateo, 1996; Gonneea et al., 2004; Kennedy et al., 2010). Additional studies using stable isotopes are warranted at these sites to explore differences in C inputs and cycling among different environmental conditions surrounding the seagrass beds.

5.1. Regional differences in C stocks among sites

The largest C_{org} stock in the GoM lies in South Florida in the lower subtropical to tropical area between the reef tracks, Florida Keys back reef, and the GoM FL shelf and Florida Bay, including the South Florida estuaries. In Texas, the highest C_{org} stocks are in the Laguna Madre, between the Padre Island National Seashore (eastern shore) and the massive King Ranch (western shore). For Mexico, precise spatial extent measurements are being formulated, but are not yet available. However, the carbon stock for this portion of the GoM is expected to be far smaller than 0.6 Tg. Neither Cuba nor the Mexican GoM has seagrass restoration attempts to-date. Of the over 1 million ha of seagrass lost in the GoM, Texas has lost a far greater proportion of its seagrass than Florida, especially in the northern, industrialized estuaries. It is clear from Appendix B that Louisiana, Alabama, and Mississippi are each close to the "tipping points" of C_{org} loss since over 80% or more of their seagrass cover has been lost over the last few decades. The State of Florida Department of Environmental Protection states losses of over one million ha. We note that if seagrass restoration were undertaken for even half of the million ha of seagrass that was previously lost, this could contribute up to an additional 12.7 Tg C_{org} to the existing 34.6 Tg of standing stock.

Such results demonstrate that, in the GoM, seagrass is a major blue carbon sink, and that restoration of seagrasses in areas that previously hosted seagrass cover in this region can offer a viable climate change mitigation strategy. Such activities have great potential for integration into carbon accounting schemes to enhance blue carbon conservation such as MRV (Monitoring, Reporting, and Verification) and for minimizing C emissions from seagrass loss through mechanisms such as REDD + carbon accounting schemes. The utility of seagrass restoration also ameliorates other ecosystem services, including bolstering fisheries, fish nursery function, and stabilizing sediments (Moberg and Rönnbäck, 2003; Barbier et al., 2011; van Katwijk et al., 2016). This study demonstrates that subtropical/tropical restored seagrass can sequester large amounts of carbon within a short time following restoration (as seen at San Luis Pass and Aransas Bay, Texas), which differs from mangroves that take some years before sequestration occurs in large amounts (DelVecchia et al., 2014). These results suggest that carbon accumulation in restored beds occurs quickly after restoration, likely through a combination of the following processes: direct sediment trapping, pumping of photosynthates into the sediments by seagrass plants, and diagenesis. This rapid C_{org} sequestration following restoration activities highlights the potential of seagrass restoration for ameliorating the effects of blue carbon losses in the GoM and elsewhere.

Florida's large seagrass C_{org} sink is probably due to a longer coast line, and because only a few short, clastic rivers drain into this part of the GoM which can cause severe turbidity and salinity alterations. The large seagrass preservation areas set aside since the 1960's (i.e., the Everglades National Park, 3 national marine estuaries, Federal EPA estuaries, and State preserves) and governmentally-enforced seagrass conservation over the last 45 years likely also contributed to the high C_{org} stocks at our Florida samples sites. Florida's program of public awareness has created a high value for seagrass among citizens and government resource managers, who demanded substantial amounts of restoration for seagrass "taking" compared to the other GoM states. As a result, Florida has less proportional seagrass loss and more ha of restored seagrass than other US GoM states (Thorhaug, 2014; Thorhaug et al., in review). Louisiana's far more extensive shoreline than Mississippi or Alabama, is dominated by marshes, is well-documented as retreating from disturbances, experiences subsidence, and is highly vulnerable to sea-level rise and intense storm-events (Handley et al., 2007). Louisiana's seagrass is presently limited to an eastern offshore extent behind the eroding Chandeleurs barrier islands in the Breton National Wildlife Refuge (Handley et al., 2007).

5.2. Loss profile for sediment depth of organic carbon

We hypothesize that a major pathway of the seagrass sediment carbon loss process is characterized by a slow physical diffusion down a gradient. The loss of carbon in the upper 10 cm is important to the discussion of core length for the "best" carbon loss measurements by Fourqurean et al. (2012a) suggest that up to 1 m of sediment may be lost when a seagrass meadow is impacted, but this one meter loss estimate remains highly debated. What our current study suggests is that rate of egress of carbon in the upper 10 cm layer occurred more rapidly than in deeper sediments 10–20 cm after the seagrass meadow was killed, and that some the sediment did not leave the site. The differences in C_{org} among the impacted barren core depth profile, the always barren carbon depth profile, and the natural seagrass profile indicate that some C_{org} loss has occurred in the impacted sites at depths upper portions of the sediment profile (0–10 cm). However, similarities at the deeper, 10–20 cm core depths among the impacted barren, restored, and natural seagrasses indicate that areas that have been previously-disturbed are likely retaining some residual carbon from the prior natural seagrass bed. These results clearly suggest that residual natural seagrass carbon in 20 cm-deep sediments may remain for decades at a site following disturbance. This contradicts the Fourqurean et al. (2012a) hypothesis of total loss of 1 m of carbon. Variability among sites could explain this discrepancy, as could differences in carbon loss following various impact events. However, there are natural and anthropogenic carbon loss factors influencing seagrass C_{org} stock and flux across the GoM, and loss pathways remain a "black box" of variables without further experimentation. High energy extreme storm events occur in areas such as Florida Bay. Rivers are major sources of CO_2 efflux (Raymond et al., 2013), and high-intensity storm events throughout the GoM also deliver large amounts of CO_2 to coastal marine systems (Bianchi et al., 2013; Hotchkiss et al., 2015; Raymond and Spencer, 2015). Yet, the effect of such sedimentation from storm events on seagrass carbon stocks, sequestration, and flux has yet to be estimated. Nor have the impacts of sediment reworking and bioturbation on C-cycling caused by animals such as *Callianassa* shrimp (Roche et al., 2016), clams, burrowing crabs, rays, and serpulid worms. Sediment microbial activity also influences carbon-cycling within natural (Ziegler and Benner, 1999; Holmer et al., 2004) and restored seagrass beds. Limited data from *T. testudinum* in Laguna Madre, Texas via phospholipid fatty acid concentrations by Jones et al. (2003) suggests that bacterial abundance is greater in vegetated communities compared to bare areas. The microbial community may be responsible for a significant component of dissolved organic carbon remineralization in seagrass beds. However, future studies that examine the role of bacteria and plankton in relation to seagrass C_{org} losses from impact and subsequent gains from restoration could facilitate a better understanding of seagrass biogeochemistry in the GoM and elsewhere (e.g., Liu et al. 2017).

Future research that investigates the rate and magnitude of C_{org} losses across the depth profile of seagrass sediments is needed. In the context of seagrass restoration, the more rapidly an impacted site is restored, the greater the potential for mitigating C_{org} losses, including stopping carbon leakage to estuarine waters. Stopping leakage is pertinent given the current debates about how deep C_{org} losses penetrate into the sediment profile (i.e. Pendleton et al., 2012), and how different environmental settings influence C_{org} flux (i.e. Marbà et al., 2015). It is theoretically possible for the entire meter to be disturbed in very high energy sites as in Perth, Australia by Marbà et al. (2015). However, our study sites occurred in the sheltered, lower energy conditions typical of GoM estuarine seagrass meadows, where not all of the top 20 cm of sediment was lost over the multi-decadal period after the impacting events. Our restorations dated from events ranging from 1945 to 2012 during an intense industrialization and urbanization period in the GoM, in which impact events were still very apparent in the raw sediment profiles.

The enclosed nature of the GoM's basin with sediment accretion throughout soft-bottom estuaries invites comparisons with other areas such as the North American Atlantic and Pacific coasts which contain seagrass at more high energy sites. For example, Lavery et al. (2013) also identified variability among C_{org} stocks when comparing both sites and species at 17 sites within a high energy section of the open Australian coastline to the Pacific Ocean, that ranged from temperate to subtropical. Such results herald the need to incorporate spatial variation in C_{org} stocks in larger-scale estimates of seagrass carbon stock and sequestration. Spatial interpolators and multivariate modeling could enhance the accuracy of such estimates by providing tools that incorporate the range of variation in C_{org} stocks into large-scale estimates.

5.3. Sedimentary carbon loss comparison between species

Our results suggest that different species can sequester different amounts of sedimentary C_{org}. For example, the sediments beneath *T. testudinum* were more carbon rich than those below *H. wrightii* which corroborates other prior research by Miyajima et al. (2015), Serrano et al. (2013) and Lavery et al. (2013) who all demonstrated that C stocks varied among Asian and Australian subtropical-Pacific seagrass species. In the GoM, *T. testudinum* has extensive root and rhizome systems known to influence C concentrations in seagrass sediments (Wetzel and Penhale, 1979; Moriarty et al., 1986). Thus, experiments that compare carbon translocation by roots to sediment for the range of dominant GoM seagrass species are needed for understanding species-level differences in C_{org} sequestration.

5.4. Impact effects on sequestration

Low salinity manipulation (diverting water for agriculture, urbanization, etc.) had negative influences on C_{org} sequestration at the Aransas Bay site. Sewage effluents in sediments were a stimulant to seagrass C_{org} sequestration, which accompanied high seagrass growth after restoration measured at this site (Thorhaug, 1987). Four of our sample sites suffered only a single impact period at the time of the "killing" of seagrass and are now preserves. Four other sites experienced continually high disturbances; these disturbed sites contained less sedimentary C_{org} carbon post-restoration than the four single-event-impact-conserved sites. Obviously, the areas of greatest impact effects are also where greatest losses of seagrass and its carbon have occurred.

5.5. Rate of seagrass organic carbon sequestration into sediment

Previous temperate studies of restored vs. natural sequestered seagrass carbon (Greiner et al., 2013; Marbà et al., 2015) did not show greater sequestration in restored seagrass when compared to natural seagrass, while our results indicated that at some sites, restored seagrass C_{org} was significantly higher than that of adjacent natural seagrass beds. Our hypothesis is that more vigorous growth of younger plants in restored seagrass beds sequesters more sedimentary carbon than older natural seagrass meadows. The age of restoration had a significant effect on carbon stocks and C_{org} sequestration rates appear larger for southern than northern GoM areas, partially due to vigorous 12-month seagrass growth at temperatures from 21 to 29 °C across the sample sites (Thorhaug and Roessler, 1977; Dunton, 1994; Livingston et al., 1998).

6. Conclusions

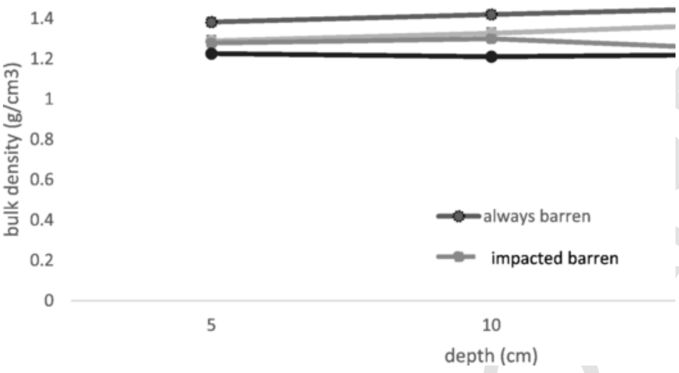
Seagrasses provide a multitude of ecosystem services across the the United States and Mexico. Our work identifies the GoM as a North American seagrass blue carbon hotspot with substantial natural seagrass C_{org} sequestration. Due to the already high C_{org} stocks in natural seagrass beds throughout the region, it also represents a prime location for seagrass restoration as a climate change mitigation strategy. Although, seagrass is abundant across much of the coastal USA, where similar calculations of this type could contribute greatly to our understanding of the potential for blue carbon accounting and restoration potential, seagrasses in temperate regions of the US may not sequester as much carbon as the subtropical/tropical GoM due to a more limited growing season and a longer history of anthropogenic stressors. The IPCC sub-panel on wetlands indicated that seagrass C_{org} data is needed for the integration of seagrass restoration in REDD + carbon mitigation. Carefully chosen sites for well-executed seagrass restoration in areas that are likely to be conserved over the long-term appear to us as solid mitigation tools for IPCC blue carbon emission factor offsets (Thorhaug et al., 2009; van Katwijk et al., 2016). We conclude that seagrass must be simultaneously conserved throughout the world and be restored in the substantial areas where seagrass has previously been lost from anthropogenic activities to avoid further sedimentary carbon losses. Both government and private sector seagrass restoration projects will be necessary for mitigating prior seagrass C_{org} losses while bolstering other ecosystem services which naturally accrue from restoration (e.g. fisheries and food-web enhancement, shoreline resilience, endangered species habitat – for Whooping Cranes, Kemp Ridley's turtles and manatee habitat, water clarity, and nutrient cycling).

Compliance with ethical standards

We, the authors, declare that we have no conflict of interest, that consent was obtained from all participants of the study, and that all necessary permits for the field sampling component of the study were obtained prior to core extraction.

Appendix A

Mean (± SE) dry bulk density of sediment at different depth below the surface in always barren, impacted barren, and natural and restored seagrass sediments in the Gulf of Mexico eight restoration sites.[1]



Appendix B

Seagrass coverages by states and sites and gains. Data for spatial extent from a series of investigators, Eleuterius and Miller (1976); Enos and Perkins (1979); Brown and Fisher (1980); Darnell et al. (1983); Iverson and Bittaker (1986); Sargent et al. (1995); Pulich (1998); Handley et al. (2007); Moncreiff (2007); Fodrie et al. (2010); Carter et al. (2011); Lewis (2011); Yarbro and Carlson (2011). Sequestration data is from seagrass restorations by Thorhaug (1974); Thorhaug (1980a); Thorhaug (1985); Thorhaug (1987); Thorhaug (2001); Thorhaug (2014) (8 sites herein), using Fourqurean et al. (2012b) data (upper 20 cm) for Florida Bay, southwest Florida, and Florida Keys.

State & sites	Spatial extent (gov't. measured) hectares	Sediment natural seagrass measured herein (C_{org} Mg ha^{-1})	Spatially "adjusted" total carbon standing stock 20 cm in area Mg C_{org}	Total C_{org}/area Tg C_{org} in 20 cm from this study
TEXAS	94,389		1,546,949	1.5
Galveston & Christmas Bays[a]	210	4.6	527	
Matagorda. Bays[a]	5840	11.82	69,029	
Sn. Anton. Bay/Aransas/St Charles[a]	3238	9.60	31,065	
Corpus & Redfish, Nueces[a]	9950	11.82	117,668	
Laguna Madre[a]	75,151	17.68	1,328,670	
LOUISIANA Chandeleurs[b]	1012	37.26	37,707	0.04
MISSISSIPPI Mississippi Sound[c]	750	21.2	17,900	0.18
ALABAMA Coasts/Mobile[+]	202	13.57	2741	0.003
FLORIDA	850,974		34,775,381	34.7
Panhandle[e,f]	15,881	37.4	593,949	
Big Bend[e]	248,850	55.66	13,850,991	
Central[e]	23,790	37.4	889,746	
Southwest[e]	30,169	32.7[g]	986,526	
Florida Bay[e]	58,804	32.7[g]	1,922,890	
Florida Keys/GoM shelf[e]	346,555	32.7[g]	11,332,349	
Atlantic Shelf[e]	57,024	37.4	2,132,697	
Turkey Point	37,620	57.05	2,146,221	
Grove Isle	21,533	34.44	741,597	
24–27th St	5374	17.73	95,281	
Julia Tuttle	5374	15.41	83,135	
Total	947,327		36,380,688 Mg C_{org}	36.4 Tg

[a] Pulich (42).

[b] Poirrier and Handley (45).

[g] Sediment carbon data from 0.20 from Fourqurean, Kendrick, Collins, Chambers and Vanderklift (9).

[c] Montcreiff (33).

[e] Yarbro and Carlson (34).

[f] Carlson and Madley (2006).

Appendix C

"Adapted" organic carbon loss estimates calculated from our seagrass organic sedimentary measurement of loss most comparable to each sub-region times spatial loss estimates by government's scientists. A list of specific zones around the Gulf of Mexico are herein used to calculate specific amounts of measured loss by Handley et al. (2007), Pulich (1998), Brown and Fisher (1980), Darnell et al. (1983), Eleuterius and Miller (1976), Moncreiff (2007), Iverson and Bittaker (1986), McNulty et al. (1962), Enos and Perkins (1979) et al.; Sargent et al. (1995), and Chardon (1976). Seagrass sedimentary carbon content data of natural seagrass beds, minus the sum of (previously impacted seagrass bed minus always barren sediment) is from Thorhaug (1980b), Thorhaug (1985), Thorhaug (1987), Thorhaug (2001), Thorhaug (2014), Thorhaug et al. (in review) (8 sites herein), using Fourqurean et al. (2012b) carbon data (upper 20 cm) for Florida Bay and surrounds.

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[1] "It is estimated that over the last 50 years, seagrass habitat losses ranged anywhere from 20% to 100% for most estuaries in the region (Handley et al., 2007)". In 1992, the Gulf of Mexico Program's Habitat Degradation Committee produced a report on the status and trends of emergent and submerged vegetated habitats in the Gulf of Mexico (Duke and Kruczynski, 1992). At that time, the total seagrass coverage in the shallow estuarine and nearshore waters of the northern GoM was estimated to be 1,019,844 ha, but offshore *Halophila* extent especially in federal waters was undefined. Thus, estimates of loss of deep water seagrass are very poorly established.

State & site	Loss spatial (govt. measured) in hectares	Loss measured herein relevant C_{org} Mg ha^{-1} in 20 cm	Spatially adjusted total loss in standing stock (Mg C_{org} in 20 cm/region)	Total C_{org} loss/Tg C_{org} in 20 cm depth per region	Source
TEXAS			8,203,618	**8.26**	
Galveston Christmas Bays	110,365	4.26	470,154		Pulich (1998)
Matagorda Bays	184,285	11.82	2,178,249		Pulich (1998)
Sn Antonio/ Aransas/St Charles	91,983	9.60	883,037		Pulich (1998)
Corpus/Redfish	78,931	11.82	932,964		Pulich (1998)
Laguna Madre	211,494	17.68	3,739,214		Pulich (1998)
LOUISIANA Iles de Chandeleurs	5366	13.57	72,817	**0.07**	Poirrier and Handley (2007)
MISSISSIPPI Mississippi Sound	6127	21.2	129,892	**0.13**	Duke and Kruczynski (1992); Handley et al. (2007), Moncreiff (2007), Eleuterius and Miller (1976), Carter et al. (2011)
ALABAMA Coasts & Mobile	930	4.26	4054	**0.004**	Iverson and Bittaker (1986); Fodrie et al. (2010); Heck et al. (2015)
FLORIDA			13,389,440	**13.39**	
North Panhandle	5335	13.57	72,395		Handley et al. (2007), Lewis (2011)
Big Bend	327,939	22.47	7,368,767		Mattson (1999), Duke and Kruczynski (1992) Iverson & Bittaker[43]
Central	22,903	37.26	851,991		Handley et al. (2007), Duke and Kruczynski (1992) Iverson & Bittaker[43]
Southwest	55,881	32.7^{++}	1,827,309		Handley et al. (2007)
Florida Bay	27,000	32.7^{++}	882,900		Robblee et al. (1991), Handley et al. (2007), Fourqurean et al. (2012b)
Florida Keys	29,749	37.26	1,108,448		Handley et al. (2007),
Atlantic shelf	5703	37.26	212,440		Handley et al. (2007)
Card Sound & south Biscayne Bay	10,000	57.12	571,200		Handley et al. (2007), (Thorhaug and Roessler, 1977); Thorhaug (1980a)
Central Biscayne Bay	5755	22.47	129,315		Harlem (1979), Handley et al. (2007), Thorhaug (1980b); Thorhaug (1987), Chardon (1976),
Lower half North Biscayne Bay.	4749	50.44	239,539		Thorhaug et al. (1979), Chardon (1976),
Upper half N. B. B	4749	3.14	14,912		Chardon (1976), Thorhaug (1987)
Total loss	**1,189,244**		21,689,597	**21.69 Tg**	

$^{++}$ Data from Fourqurean et al. (2012a) is used herein in Florida Bay and Southwest Florida for the upper 20 cm of the total 1 m of the core (163.5 Mg for 1 m) to make data consistent with the loss sampling unit of 20 cm.

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